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Did Recurrent Selection for Yield Affect Iowa Stiff Stalk Synthetic Maize Population Grain Fill Characteristics?

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Did recurrent selection for yield affect Iowa stiff stalk synthetic maize population grain fill characteristics

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CHAPTER 1. GENERAL INTRODUCTION

The demand for grain used for food, feed, fuel, and fiber production will increase substantially over the next 30 years (Duvick and Cassman, 1999). Meeting these projected demands by increasing land area in production is not feasible because of decreased availability of arable land, which is increasingly converted to urban, industrial, and recreational uses (Duvick and Cassman, 1999). The trend is expected to continue as population increases. One food, feed, fuel, and fiber supply-demand model presented in Rosegrant et al., (1999) predicts maize demand will increase from 526 million tons to 783 million tons from the years 1993 to 2020. If maize production area remains the same, an annual growth rate in maize yield of approximately 1.5 % is needed to meet this demand (Duvick and Cassman, 1999).

Chapter two is a review of the literature discussing grain filling characteristics in maize, and the factors that affect these characteristics. Chapter three is the main experimental portion of the thesis. Chapter three discusses the experiment conducted to address the changes that have occurred in the grain fill characteristics in the Iowa Stiff Stalk Synthetic maize population as the result of recurrent selection for yield.

Since the 1930's hybrid maize yields have risen from 1.5 Mg ha^{-1} to 8.5 Mg ha^{-1} (Duvick, 2005b). On average, 50% of these increases are due to management and 50% due to plant breeding (Duvick, 2005b). Selection for increased yield has often been accompanied by changes in other traits. Changes of these traits are often due to direct selection including tolerance to biotic and abiotic stresses, but often occur without intention by plant breeders (Duvick, 2005b). Traits that may have changed as a result of selection for yield include reduced plant and ear height, more upright leaves, reduced tassel size, delayed leaf senescence, reduced number of tillers, reduced anthesis-silking interval, reduced stalk and root lodging, tolerance to biotic and abiotic stresses, and longer period of grain fill (Duvick, 2005a). Hybrid maize yield increases may be more sustainable and easily achieved with a better understanding of the effect of individually or combinations of traits on maize yields.

Grain fill rate and duration are important determinates of maize grain yield (Gambin et al., 2007; Poneleit and Egli, 1979). The relationship between final kernel weight, kernel fill rate, kernel fill duration, and final grain yield in maize is not fully understood. There are conflicting arguments in the literature regarding the relationship between kernel fill rate, kernel fill duration, and the final yield of maize. Increasing the kernel fill rate and kernel fill duration can both lead to yield increases, but it is not well understood which factor is more important in contributing to yield increases. This experiment was designed to study the effect of recurrent selection on grain fill characteristics in maize, and how planting density affects these characteristics.

The first treatment in this study was different cycles of selection representing different levels of population advancement from the Iowa Stiff Stalk Synthetic maize population. The Iowa Stiff Stalk Synthetic Population was established by intermating 16 lines of primarily Reid Yellow Dent background with above average stalk quality. From the initial population two independent methods of selection have been carried out since 1939 (Lamkey, 1992; Sprague, 1946). The two programs of selection include half-sib selection and reciprocal recurrent selection using increased grain yield as the primary selection criteria (Hagdorn et al., 2003).

The Iowa Stiff Stalk Synthetic Population was used in this experiment because it provides a good model for the selection process that has occurred in commercial maize hybrids. The Iowa Stiff Stalk Synthetic maize population has made many important contributions to the hybrid maize seed industry including inbreed lines B14, B37, B73, and B84 (Darrah and Zuber, 1986). These inbreeds made up 19% of all parent material in hybrid maize in 1980 (Lamkey et al., 1991).

The second treatment in this study was planting density. Planting densities are one of the most important management decisions in determining final yield in maize (Sangoi, 2001). Plant densities for maximum grain yield vary, depending on water availability, soil fertility, maturity rating, planting date, and row spacing (Sangoi, 2001). The planting density at which maximum grain yield occurs in has changed dramatically in hybrids over the past several decades. Hybrids grown in the 1960's reached their maximum yield potential at about 3 plants m^{-2} while plants grown in the 2000's do not reach their maximum potential until they reach a density of 5 to 6 plants m^{-2} (Hammer et al., 2009).

We hypothesize that recurrent selection for increased yield in the Iowa Stiff Stalk Synthetic maize population has changed grain fill characteristics and the response of these characteristics to planting density. To test this hypothesis, a model was identified to characterize grain filling in maize. Parameters were extracted from this model and analyzed to compare characteristics grain filling of the treatments.

The demand for maize will continue to increase over the next 30 years (Duvick and Cassman, 1999). Therefore, it is important to ensure that maize production continues to increase to meet this growing demand. The goal of this research is to investigate the influence of recurrent selection in the Iowa Stiff Stalk Synthetic maize population, and determine the effect of plant density on grain filling in this population with the hope of improving breeding strategies and management practices to increase grain yield.

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CHAPTER 2. REVIEW OF LITERATURE

Grain Development in Maize

Understanding maize grain development may be important for improving management practices and developing alternative breeding strategies to increase maize yield. Grain fill is characterized by the rapid cell division in kernels, accompanied by the translocation of photosynthate to these kernels.

Grain dry matter accumulation is often divided into three phases; the lag, the effective grain fill, and the phase of rapid moisture loss in the kernel. The lag phase of development is a period of rapid endosperm cell division, DNA replication, and cell wall formation (Jones et al., 1984). The lag phase typically covers a period from about 0-15 days after pollination, and very little dry matter is accumulated. This phase is important because an early sink potential is established (Borras et al., 2009). The lag phase is followed by rapid starch accumulation known as the effective grain fill period. The effective grain filling period begins about 7-14 days after mid-silk and accounts for 5-95% of dry matter accumulation (Daynard et al., 1971). During this period water content continues to rise until mid-grain fill, and then decreases as dry matter content increases. The effective grain fill period is often characterized as the most important phase in grain filling in maize because it accounts for over 90% of dry matter accumulation in the kernel (Daynard et al., 1971). The third phase begins at physiological maturity. This phase is characterized by the end of dry matter accumulation, and decrease moisture in the kernel.

Maize grain yield is determined by the number of grains per unit area multiplied by the weight of those grains. Although there is often more variation in final kernel number than kernel weight, kernel weight does impact final grain yield (Borras et al., 2009). Two factors influencing final kernel weight are the rate and duration of kernel filling (Borras and Gambin, 2010; Borras et al., 2003; Poneleit and Egli, 1979). The kernel fill rate and duration varies greatly among hybrids and inbred lines of maize (Borras and Gambin, 2010; Poneleit and Egli, 1979). It is evident that more work is needed to understand the importance of kernel fill rate and duration on maize yield.

Effect of kernel fill rate and duration on yield. The rate and duration of kernel filling are considered important determinates of maize grain yield and both may be used as indirect yield selection criteria (Hartung et al., 1989). Selecting for earlier mid-silk date and increased kernel weight may indirectly select for increased grain filling duration and rate (Wang et al., 1999). However, there are conflicting reports in the literature about whether the rate or duration of kernel fill is more important in the final kernel weight and yield in maize. For example, Poneleit and Egli (1979) and Crosbie and Mock, (1981) argue that the duration of grain fill is more important in determining final kernel weight and yield of maize, while Borras et al. (2003) contend kernel fill rate is more important. The results of these studies may differ because of different genetic material used, the location at which the plots were grown, and the procedures used to calculate rate and duration of grain filling. Differences in the genetic material used in the studies are probably the most important factor creating differences in the results between the two studies.

Changes in kernel fill rate and duration with yield increases. Maize yield increases have come mainly by increasing the tolerance to planting density and lengthening the grain-filling period (Wang et al., 1999). When comparing maize hybrids, Wang et al., (1999) found that increasing kernel fill rate and duration, both increased final grain yield in maize, and that both may be used for indirect selection for yield. Newer hybrids are believed to yield more than older hybrids due to an increased duration of kernel fill rather than an increased rate of kernel fill (Crosbie and Mock, 1981). Crosbie and Mock, (1981) determined grain fill duration of different cycles of selection from the Iowa Stiff Stalk Synthetic maize population by calculation the days between 50% pollination and black layer. Grain fill rate was determined by dividing grain weight per plant by the grain fill duration of that plant. Longer grain-filling durations have come from delaying physiological maturity rather than changing flowering date (Cavalieri and Smith, 1985). The harvest moisture has also remained the same allowing hybrids to remain in the same maturity group (Cavalieri and Smith, 1985; Gambin et al., 2007). This is important to ensure efficient and timely harvest of newer hybrids with delayed physiological maturity.

Factors Affecting Grain Fill

Source-sink relationships. Maize yield can be limited by the source of assimilates or the number and size of sinks or kernels available. In most growing conditions maize is considered a sink limited crop (Borras et al., 2004). Maize is considered source limited if resource assimilates are dramatically decreased during grain filling (Borras et al., 2004). Borras et al., (2004) altered the amount of assimilate supply per kernel by limiting the number of kernels per ear at flowering. The number of kernels was controlled by limiting the number of pollinations made. By limiting the number of kernels per plant, the amount of source per sink is being increased. Reductions in source strength during grain filling decreases final kernel weight significantly while increases in source availability per kernel show only slight increases in final kernel weight (Borras et al., 2004). Increases in potential maize kernel weight can only be achieved by increasing the sink strength or source availability during the effective grain fill period.

Source capacity during grain filling in maize is determined by the photosynthetic rate and the amount of carbohydrate reserves in the plant (Uhart and Andrade, 1991). Unlike crops such as sunflower or soybean, maize maintains its ground cover and photosynthetic capacity almost to physiological maturity (Andrade, 1995). Any biotic or abiotic stress that limits this source availability during grain filling such as low temperature, low radiation, disease, or defoliation by insects or hail may have adverse effects on maize yield per plant (Andrade and Ferreiro, 1996). Andrade and Ferreiro, (1996) determined the effect of altered source levels on the rate and duration of grain fill in maize. Andrade and Ferreiro, (1996) determined that increasing or decreasing the source level per plant had no effect on grain fill rate, while decreasing the amount of source per plant shortened grain fill duration. This is evidence that in a source limited environment, grain yield is reduced due to shortened grain fill duration, rather than a decreased rate of grain fill.

Kernel number. Kernel number is closely associated with grain yield in maize. The number of kernels per ear may have an effect on kernel fill rate, kernel fill duration, and final kernel weight in maize (Borras and Otegui, 2001). An increase in kernel number is associated with decreased kernel weight in maize (Borras and Otegui, 2001). When comparing maize hybrids, Borras and Otegui, (2001) discovered the decrease in kernel weight comes from a reduced kernel fill rate rather than a shortened effective grain fill period. The decrease in kernel weight is believed to come from a decreased assimilate supply per kernel, suggesting that there is a tradeoff between kernel number and final kernel weight in maize (Uribelarrea et al., 2008).

Leaf senescence. Leaf senescence is the deteriorative process that leads to the loss of leaf function. Decreased senescence may be partially responsible for increased yields in newer maize hybrids compared to older hybrids (Crosbie and Mock, 1981). Leaf senescence is important in maize grain fill because it affects yield by decreasing the active photosynthetic area which decreases the amount of assimilate available for growing kernels (Wolfe et al., 1988). Increasing the time a crop maintains its active photosynthetic area may be one way to increase yield in maize (Craftsbrandner and Poneleit, 1992). The green leaf area duration, which measures the rate of senescence is highly correlated with final kernel dry weight (Wolfe et al., 1988). Low water stress and nitrogen stress can increase the rate of senescence and decrease the amount of photosynthate available for growing kernels, resulting in lower final kernel weights (Wolfe et al., 1988). Newer hybrids have increased yield in part due to a decreased rate of leaf senescence during grain filling (Tollenaar and Wu, 1999). This may be due to an increased source: sink ratio during grain filling (Tollenaar and Wu, 1999).Craftsbrandner and Poneleit, (1992) found that populations with shorter effective filling periods senesce earlier, while populations with longer effective filling periods senescence later. This provides some evidence that the timing of senescence may be associated with the length of the effective grain filling period.

Plant density. Poneleit and Egli, (1979) compared the effect of stand density on two maize inbreeds. Poneleit and Egli, (1979) reported that increases in stand density had no significant effect on kernel fill rate. The kernel fill duration of the two inbreeds were shortened by 2.5 days at increased densities. This led to smaller kernels as well as fewer kernels resulting in a 20% yield decrease (Poneleit and Egli, 1979). Borras et al. (2003) studied the effect of planting density on two maize hybrids. Borras et al. (2003) reported reductions in final kernel weight due decreases in kernel filling rate rather than a shorter kernel fill duration. Therefore, more work is needed to determine the effect of planting density on the rate and duration of grain filling in maize.

Plant growth rate. Maize yield is often associated with the rate of plant biomass accumulation and the partitioning of assimilates into developing grain (Severini et al., 2010). Plant growth rate is very important in determining the final kernel number and weight of maize (Gambin et al., 2008; Severini et al., 2010). Increased plant growth rates are partially responsible for increased final kernel weight and number (Gambin et al., 2008; Severini et al., 2010). Gambin et al., (2008) modified plant growth rate by thinning the final stand of a maize population before reproductive growth and found that increased plant growth rates during flowering had positive effects on final kernel number and weight, while increased plant growth rate during the effective filling period had no significant effects on final kernel number or weight.

Heat stress. Heat stress during grain filling affects grain growth and yield in maize (Cheikh and Jones, 1994). The average temperature in the U.S. Corn Belt during the grain filling period in maize is often above the optimum temperature for maize development. Therefore, maize is often under heat stress during the grain filling period of development (Wilhelm et al., 1999). Heat stress before and during reproductive growth often increases the amount of total biomass in maize (Chen et al., 2010). This may be the result of an increased amount of vegetative growth, but a decreased amount of reproductive growth. However, heat stress often leads to decreased ear weights due to a decrease in assimilate transport and partitioning to the ear from the leaves (Chen et al., 2010). Although heat stress has many adverse effects in the plant, heat stress during grain filling may interfere with endosperm starch biosynthesis which may result in smaller kernels. Heat stress affects grain filling by lengthening the grain fill duration on a heat unit basis, but slows the grain fill rate resulting in a decreased kernel weight (Wilhelm et al., 1999). This decrease in kernel weight is due to the slowing of starch storage processes and select enzymes of starch metabolism (Wilhelm et al., 1999).

Drought stress. Drought stress accounts for a significant proportion of yield losses in maize each year (Nesmith and Ritchie, 1992). Drought stress during pollination increases the interval between silk emergence and pollen shedding resulting in increased barrenness and decreased kernels per ear (Herrero and Johnson, 1981). Drought stress during grain filling can also be detrimental to final yield in maize. Drought stress during pollination can increase the interval between silking and pollen shed up to 3-4 days (Herrero and Johnson, 1981). Drought stress during grain filling in maize does not result in a decreased final kernel number, but results in a decrease in final kernel weight (Westgate, 1994). The loss in kernel weight results from a shortened effective grain fill period, while the rate of kernel growth remains the same (Nesmith and Ritchie, 1992; Westgate, 1994). The decreased duration of the effective grain fill period partially due a decreased embryo volume, which leads to less dry matter accumulation in the embryo(Westgate, 1994). Drought stress during grain filling may also lead to early senescence (Nesmith and Ritchie, 1992). This leads to less green leaf area and biomass during grain filling which results in decreased source (Nesmith and Ritchie, 1992).

Yield Increases in Maize

Hybrid maize grain yields have increased in the past 75 years. Grain yields began to increase in the 1930's and have increased an average of 65-75 kg/ha per year (Duvick, 2005a). It is believed that yields have increased due to both genetic and agronomic management practices. Tollenaar and Lee, (2002) states that most of this yield increase can be attributed to an improved genetic by management interaction. Most of the increase in genetic gains can be attributed to an increased tolerance to biotic and abiotic stresses as well as an increased tolerance to high planting densities (Tollenaar and Wu, 1999). Stress is the altered physiological condition caused by factors that tend to alter equilibrium in the plant (Gaspar et al., 2002). Genetic gains have also been seen in physiological changes in traits that promote efficiency in growth, development, and partitioning in the plant (Duvick, 2005b). Changes in these traits have come from direct selection by breeders, and in some cases without any intentions from breeders (Duvick, 2005b). Traits that accompanied genetic gains in yield include; reduced plant and ear height, more upright leaves, reduced tassel size, delayed leaf senescence, reduced number of tillers, reduced anthesis-silking interval, reduced stalk and root lodging, tolerance to biotic and abiotic stresses, and longer period of grain fill (Duvick, 2005b).

Planting Density

Planting densities are one of the most important management decisions in determining final yield in maize (Sangoi, 2001). Plant densities for maximum grain yield vary, depending on water availability, soil fertility, maturity rating, planting date, and row spacing (Sangoi, 2001). Plant density affects plant architecture, alters growth and development patterns, and influences carbohydrate production and partitioning (Casal et al., 1985).

Planting densities affects maize development during both vegetative growth and reproductive growth (Tetiokagho and Gardner, 1988a; Tetiokagho and Gardner, 1988b). Increasing plant density affects vegetative growth by increasing leaf area index and vegetative dry matter, but alters light distribution by increasing the amount of light intercepted by the upper canopy and tassel, and decreases the amount of light received by the lower canopy (Tetiokagho and Gardner, 1988a). Increased planting density affects reproductive growth by increasing barrenness and silking to anthesis interval (Buren et al., 1974). Selection practices aimed to improve these traits in maize have increased its tolerance to high stand densities.

Planting density is one of the most important factors in determining final yield in maize. Newer maize hybrids tolerate higher plant densities better than older hybrids; therefore plant density recommendations have increased in recent years (Hammer et al., 2009; Tollenaar, 1991). Maximum yield potential cannot be reached without the proper planting density for a particular hybrid. Hybrids grown in the 1960's reached their maximum yield potential at about 3 plants m^{-2} while plants grown in the 2000's do not reach their maximum potential until they reach a density of 5 to 6 plants m^{-2} (Hammer et al., 2009).

When comparing recent maize hybrids to older hybrids, (Tollenaar and Lee, 2002) discovered that yield differences between the hybrids was only noticed at high planting densities. Therefore, Tollenaar and Lee, (2002) state that maize yield increases can be mostly attributed to increased tolerance to high planning densities. There are many reasons more recent hybrids are more tolerant to high planting densities than older hybrids. Genetic gains have led to lower plant to plant variability has led to newer hybrids having increased stress tolerance than older hybrids (Tollenaar and Wu, 1999). The increase in stress tolerance is a result of more efficient resource capture and use in newer hybrids than older hybrids (Tollenaar and Wu, 1999). Increasing planting density is one method of increasing interception of incoming solar radiation in maize (Buren et al., 1974). The increase in interception of solar radiation comes from an increase in Leaf Area Index (LAI). The higher LAI results in more interception of photosynthetically active radiation and more dry matter accumulation during vegetative growth (Tollenaar and Aguilera, 1992). Another reason for increased tolerance to higher planting densities in newer hybrids is increased crop growth rates. Tollenaar et al., (1992) studied hybrids from three different decades to determine the effect of planting density on plant growth rate and grain growth. When planted at higher densities, this report noted that newer hybrids had higher crop growth rates from one week before silking to three weeks after silking than older hybrids (Tollenaar et al., 1992). The increased crop growth rate led to more assimilates being produced which resulted in a greater number of kernels per plant, greater kernel weight, and higher yields in newer hybrids than older hybrids (Tollenaar et al., 1992). An increased crop growth rate resulted in a more synchronized silking anthesis interval, which led to less barrenness and a greater number of kernels in more recent hybrids (Tollenaar et al., 1992). Other traits that may increase a hybrid's tolerance to high planting densities include lower dry matter partition to the tassel resulting in a more balanced relationship between male and female inflorescence, a more compact canopy with shorter plants and more upright leaves for enhances solar radiation interception, and lower ear and plant height resulting in decreased stalk lodging (Sangoi et al., 2002).

Iowa Stiff Stalk Synthetic Population

Formation of population. The Iowa Stiff Stalk Synthetic (BSSS) maize population was developed in 1934 by intermating 16 inbred lines of primarily Reid Yellow Dent Background with above average stalk quality (Lamkey, 1992; Sprague, 1946). The BSSS has now undergone over 50 years of recurrent selection and has been the base for two independent selection programs (Holthaus and Lamkey, 1995). The two selection programs include half-sib recurrent selection and reciprocal recurrent selection using increased grain yield and decreased harvest moisture as selection criteria (Hagdorn et al., 2003). The half-sib selection program was carried out using seven cycles of half sib selection with the double-cross tester Iowa 13 (Lamkey, 1992). The population was then renamed BSSS(HT)C7. From that population the 29 best performing lines were selected and created the population BS13(S)C0 (Holthaus and Lamkey, 1995). BS13(S)C0 underwent five cycles of half-sib selection using B97 as a tester to create the population BS13(HI)C5 (Edwards, 2010). The reciprocal recurrent selection program used BSSS and the Iowa Corn Borer Synthetic as base populations for selection (Holthaus and Lamkey, 1995). Reciprocal recurrent selection is used to simultaneously improve both populations used for inbred selection while keeping genetic variability.

Importance of BSSS. Public inbred lines have played an important role in the improvement of maize (Gethi et al., 2002). The Iowa Stiff Stalk Synthetic Population has contributed many important inbreeds to hybrid maize including B14, B37, B73, and B84 (Lamkey et al., 1991). In 1980 these made inbreeds made up 19% of all parent material for maize grown in the United States.

Genetic improvement in BSSS. Recurrent selection is a breeding procedure used to increase the frequency of favorable alleles in a given population. Increasing the frequency of favorable alleles will increase the probability of obtaining superior inbred lines for hybrid maize (Lamkey, 1992). The Iowa Stiff Stalk Synthetic Population has undergone recurrent selection since 1939 and experienced many changes in traits (Lamkey, 1992). The average rate of response after seven cycles of half-sib selection using Iowa 13 as a tester for yield was 3.9% per cycle (Lamkey, 1992). The six cycles of

S_2did not significantly change yield (Lamkey, 1992). Evaluation of the reciprocal recurrent selection program indicated improvements in grain yield of 4.6% per cycle as a result of reciprocal recurrent selection and a testcross gain of 1.65% (Eberhart et al., 1973). Keeratinijakal and Lamkey, (1993) reported a testcross increase of 2.8% in the first 11 cycles of selection in the reciprocal recurrent selection program. Brekke et al., (2010) found that advanced cycles of the Iowa Stiff Stalk Synthetic maize population had higher grain yields than the initial cycle BSSS when grown at increased plant densities. Reductions in the silking anthesis interval, plant heights, and leaf numbers were noticed in advanced cycle compared to the unimproved base population BSSS when grown at high planting densities (Brekke et al., 2010).

BSSS. The Iowa Stiff Stalk Synthetic (BSSS) maize population was developed in 1934 by intermating 16 inbred lines of primarily Reid Yellow Dent Background with above average stalk quality (Lamkey, 1992; Sprague, 1946). BSSS become the base population for two independent breeding programs (Holthaus and Lamkey, 1995).

BSSS(R)C17. This population is the 17^{th} cycle of the reciprocal recurrent selection program. This program used Iowa Stiff Stalk Synthetic and Iowa Corn Borer Synthetic as base populations for reciprocal recurrent selection (Holthaus and Lamkey, 1995).

BS13(HI)C5. Starting with the population BSSS seven cycles of half-sib selection using Iowa 13 as a tester were completed the population was renamed BSSS(HT)C7 (Holthaus and Lamkey, 1995). From that population, the 29 best performing lines were selected creating the population BS13(S)C0 (Holthaus and

Lamkey, 1995). Five cycles of half-sib selection using B97 as a tester resulting in the population BS13(HI)C5 (Edwards, 2010).

BSCB1. The Iowa Corn Borer Synthetic no. 1 (BSCB1) was synthesized from 12 lines with resistance to whorl feeding by European corn borer (Keeratinijakal and Lamkey, 1993). BSCB1 was selected along with BSSS for reciprocal recurrent selection in order to improve both cycles simultaneously (Holthaus and Lamkey, 1995).

Grain Growth Modeling

Previous effort has been made to model grain growth in maize. Models previously used to model grain fill include linear models, Poneleit and Egli, (1979) and bilinear models(Gambin et al., 2007). Very little work has been done on the fitting of non-linear models to grain growth in maize. There are many advantages to using a non-linear model for growth data rather than a linear model. Linear models only include the observed relationship between the response variable and covariates (Pinheiro and Bates, 2000). This allows linear models to only make predictions concerning the observed range of data. Non-linear models often include theoretical characteristics of the data such as asymptotes that linear models do not (Pinheiro and Bates, 2000). This allows non-linear models to make more accurate predictions outside the observed range of data than a linear model.

Logistic function. The logistic function is a non-linear, symmetrical, three parameter, sigmoidal curve often used to model growth in organisms(Pinheiro and Bates, 2000). The equation for the logistic model is as follows:

$$F(\mathrm{t}) = \Phi_1 / \{1+\exp[-(\mathrm{t}-\Phi_2)/\Phi_3]\}$$

This equation represents growth as it relates to time (t). The parameter Φ_1 represents the asymptotic height of the model. The second parameter (Φ_2) is known as the x-midpoint and is the time for the model to reach half of their asymptotic height. This is the point on the curve in which rate of growth changes from increasing to decreasing. The third parameter(Φ_3) is the time elapsed between the model going from 50% to 75% of its asymptotic height (Pinheiro and Bates, 2000).

Gompertz function. The gompertz function is a non-linear sigmoidal curve often used to model growth (Franses, 1994). The gompertz function is considered non-symmetrical when compared to the logistic function (Franses, 1994). The gompertz curve assumes the period of initial increasing growth is shorter than the period of decreasing growth prior to the saturation point (Franses, 1994). The gompertz function has two characteristics that distinguish it from other functions. The first is the point of inflection in which the rate of growth goes from increasing to decreasing always occurs before the half way point to the asymptote (Franses, 1994). The second characteristic is that the rate of growth is always greater than zero until it eventually slows to zero (Franses, 1994). The equation for the gompertz function is as follows:

$$g(\mathrm{t}) = \mathrm{a}^{\mathrm{b}(\exp(\mathrm{ct}))}$$

In this equation *Y* represents growth at a given time value (t). This equation consists of three unknown parameters a, b, and c. A is equivalent to the upper asymptote of the curve. Both b and c are negative numbers and represent the x displacement and the scale respectively.

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CHAPTER 3. THE EFFECT OF RECURRENT SELECTION FOR YIELD ON GRAIN FILL CHARACTERISTICS IN THE IOWA STIFF STALK SYNTHETIC MAIZE POPULATION.

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ABSTRACT

Hybrid maize yield increases, new product development, and increased stress tolerance can be more easily achieved with a better understanding of the physiological and genetic basis for phenotypic changes in response to recurrent selection for yield. The purpose of this study was to identify changes in grain fill characteristics and their interaction with plant density in a closed population and identify a model that accurately predicts grain fill in this population. We hypothesize that recurrent selection for increased yield indirectly impacted the grain fill characteristics of maize including final kernel weight, kernel fill duration, and kernel fill rate in the Iowa Stiff Stalk Synthetic maize population. We also hypothesize that recurrent selection for yield has indirectly improved maize tolerance to high plant density stress for these grain fill characteristics.

Populations representing different levels of advancement from the Iowa Stiff Stalk Synthetic maize population were compared to at two different locations near Ames, Iowa in 2009 and 2010. Populations were compared at plant densities of 5.3 and 7.7 seeds m^{-2}. Treatments were replicated three times per location in a split plot design. Recurrent selection for yield has led to changes in final kernel weight and kernel fill duration, as well as the response of kernel weight to increased planting densities. This

supports our hypothesis that recurrent selection for yield changed grain fill characteristics and the effect of high plant density stress in the Iowa Stiff Stalk Synthetic maize population. The rate of kernel fill was not affected by recurrent selection for yield in the Iowa Stiff Stalk Synthetic maize population.

INTRODUCTION

The demand for food, feed, fuel, and fiber will increase substantially over the next 30 years. Increasing land area in production is limited by the amount of arable land lost to urban, industrial, and recreational uses (Duvick and Cassman, 1999). Maize demand will also increase in future years. Without the increase in maize production area, an annual yield increase of 1.5% is needed in order to meet the growing demand (Duvick and Cassman, 1999).

Maize yields have risen continually since the 1930's. Since that time, hybrid maize yields have increased from 1.5 mg ha^{-1} to 8.5 mg ha^{-1} (Duvick, 2005b). On average, approximately 50% of these increases are due to management and 50% are due to plant breeding. Increases in yield are often accompanied by changes in other traits (Duvick, 2005b). Changes in these traits are sometimes due to direct selection, but often occur without intention by plant breeders (Duvick, 2005b). Traits that may have changed as a result of selection for yield include reduced plant and ear height, more upright leaves, reduced tassel size, delayed leaf senescence, reduced number of tillers, reduced anthesis-silking interval, reduced stalk and root lodging, tolerance to biotic and abiotic stresses, and longer period of grain fill (Duvick, 2005a). Hybrid maize yield increases may be more easily achieved with a better understanding of the effect of selection for yield on these traits.

The final yield of maize is determined by the final number of kernels and the weight of those kernels. Although there is much more variation in kernel number, kernel weight is important to final maize yield. Kernel fill rate and duration are important factors in determining final yield in maize (Gambin et al., 2007; Poneleit and Egli, 1979). Increased kernel fill rate and duration will both result in yield increases, but it is unclear which factor has been more influential in increasing grain yield in maize. There are conflicting arguments in the literature regarding the relationship between final kernel weight, kernel fill rate, kernel fill duration, and final grain yield in maize. Poneleit and Egli, (1979) report that grain fill duration is more important in yield determination in maize, while Borras et al. (2003) contends that the rate of grain filling is more important. It is evident that more work is needed to determine the effect of these grain fill characteristics on the final yield of maize.

The Iowa Stiff Stalk Synthetic Population was developed by intermating 16 lines of primarily Reid Yellow Dent background with above average stalk quality. From the initial population two independent methods of selection have been carried out since 1939 (Lamkey, 1992). The two programs of selection include the half-sib selection and reciprocal recurrent selection programs which both used increased grain yield as the primary selection criteria (Sprague, 1946). The half-sib selection program consisted of seven cycles of half-sib selection using IA13 as a tester. The population was then renamed BSSS(HT)C7 (Holthaus and Lamkey, 1995). From this population, the 29 best preforming S_1 lines were selected creating the population BS13(S)C0 (Lamkey, 1992).

This population underwent 5 cycles of half-sib selection using B97 as a tester creating the population BS13(HI)C5 (Edwards, 2010). The reciprocal recurrent selection program used reciprocal recurrent selection using the Iowa Stiff Stalk Synthetic and Iowa Corn Borer Synthetic as base populations which continues today (Lamkey, 1992). Reciprocal recurrent selection was used to simultaneously improve both populations while keeping genetic variability. The Iowa Stiff Stalk Synthetic Population was used in this experiment because it provides a good model for the selection process that has occurred in commercial maize hybrids. The Iowa Stiff Stalk Synthetic maize population has made many important contributions to the hybrid maize seed industry including inbreed lines B14, B37, B73, and B84 (Darrah and Zuber, 1986). These inbreeds made up 19% of all parent material in hybrid maize in 1980 (Lamkey et al., 1991).

The demand for maize will continue to increase over the next 30 years (Duvick and Cassman, 1999). Therefore, it is important to ensure that maize production continues to increase to meet this growing demand. The objective of our experiment is to study the effect of recurrent selection for increased yield on grain fill characteristics in the Iowa Stiff Stalk Synthetic population, and gain a better understanding of effect of planting density on these characteristics. A better understanding of the effect of selection for increased yield on grain fill characteristic could lead to improved breeding practices for the indirect selection for increased yield and tolerance to high planting densities in maize. The other objective of this study was to identify a function that accurately models grain filling in the Iowa Stiff Stalk Synthetic Population. A better understanding of the effect of recurrent selection on yield, and the effect of plant density on grain filling may lead to improved breeding strategies and management practices for increasing grain yield in maize.

MATERIALS AND METHODS

Three different populations representing different cycles of advancement from the Iowa Stiff Stalk Synthetic maize population were used as one of two treatments in this study. The remaining five pedigrees represent F-1 crosses between populations, or a cross with the Iowa Corn Borer Synthetic Population (BSCB1).

BSSS. The Iowa Stiff Stalk Synthetic (BSSS) maize population was developed in 1934 by intermating 16 inbreed lines of primarily Reid Yellow Dent Background with above average stalk quality (Lamkey, 1992; Sprague, 1946). This has become the base population for two independent breeding programs (Holthaus and Lamkey, 1995).

BSSS(R)C17. This population is the 17th cycle of the reciprocal recurrent selection program. This program used Iowa Stiff Stalk Synthetic and Iowa Corn Borer Synthetic as base populations for reciprocal recurrent selection(Holthaus and Lamkey, 1995).

BS13(HI)C5. Starting with the population BSSS seven cycles of half-sib selection using Iowa 13 as a tester were completed the population was renamed BSSS(HT)C7 (Holthaus and Lamkey, 1995). From that population, the 29 best performing lines were selected creating the population BS13(S)C0 (Holthaus and Lamkey, 1995). Five cycles of half-sib selection using B97 as at tester resulting in the population BS13(HI)C5 (Edwards, 2010).

BSCB1. The Iowa Synthetic Corn Borer no. 1 (BSCB1) was synthesized from 12 lines with resistance to whorl feeding by European corn borer (Keeratinijakal and Lamkey, 1993). BSCB1 was selected along with BSSS for reciprocal recurrent selection in order to improve both cycles simultaneously (Holthaus and Lamkey, 1995).

BSSS/BSSS(R)C17. The population BSSS crossed with the BSSS(R)C17 population.

BSSS/BS13(HI)C5. The population BSSS crossed with the BS13(HI)C5 population.

BSSS/BSCB1. The population BSSS crossed with the BSCB1 population.

BSSS(R)C17/BSCB1. The population BSSS(R)C17 crossed with the BSCB1 population.

BS13(HI)C5/BSCB1. The population BS13(HI)C5 crossed with the BSCB1 population.

The second treatment in this study was planting density. The planting densities used in this study were 5.3 and 7.7 seeds m^{-1}. The final stand for the high density and low density treatments were 4.7 and 6.6 plants m^{-1} respectively.

Experimental Design

Field experiments were conducted at two locations near Ames, Iowa in 2009 and 2010. Plots were panted on May 5 and May 7 in 2009 and April 29 and May 4 in 2010. Plots were planted in a split plot design with planting density as the whole plot treatment and breeding population as the sub-plot treatment. Each experimental unit consisted of four rows 5.49 meters in length and spaced 0.762 meters apart.

Plants were tagged prior to reproductive growth so that the silking date of each plant could be recorded. Two plants from each plot were harvested at weekly intervals beginning 15 days after silking. Ears from each plant were collected and transported to the lab in air tight bags. The harvest of ten kernels was accomplished from each ear at spikelet positions 10-15 from the base of the ear 0inside of a humidified box (Borras et al., 2003). Ears with incomplete kernel set at the sampled portion of the ear were discarded. Kernels were dried at 70° Celsius until dry weight remained constant.

Data Analysis

A non-linear logistic model was fitted to the data and used to describe growth of maize kernel over the period of grain filling. Growing degree days were used to measure time over the grain filling period. The logistic model was chosen over the gompertz model based on the Bayesian information criterion, as well as the usefulness of the parameters of the logistic model. The equation for the logistic model is as followed:

$$y_{mnrq(r)} = \phi_{mnrq(r)} \;/\; \{1+\exp[-(x- \phi_{mq}) \;/\; \phi_{m}]\} + \varepsilon_{mnrq(r)}$$

The equation represents the kernel dry weight ($y_{mnrq(r)}$) in grams/10 kernels at a particular time(x) during grain growth in growing degree days. Parameters of the model were estimated using the maximum likelihood procedure. The first parameter ($\phi_{mnrq(r)}$) represents the asymptote of the curve. This parameter gives us an estimate of the final dry weight of the kernels. The second parameter ($\phi_{mq(r)}$) represents the inflection point and is referred to as the x-midpoint. This is the point on the x-axis in which the curve is 50% complete. At this point kernels have reached half of their final dry weight. When using the logistic function, the x-midpoint is also the point of maximum rate of dry matter accumulation (Pinheiro and Bates, 2000). The $\phi_{mq(r)}$ parameter gives us an estimate of kernel fill duration. The third parameter (ϕ_m) or scale is the time elapsed for kernel filling to go from 50% to 75% complete (Pinheiro and Bates, 2000).

Modeling Procedure

The complete modeling procedure is outlined in Pinheiro and Bates, (2000). The fullest possible model for any of the parameters in the logistic model is as followed. In this model fixed effects are represented by Greek letters, and random effects are represented by Roman letters:

Model for non-linear parameters:

$\phi_{mnrq(r)} = \mu + \alpha_m + \gamma_n + \alpha\gamma_{mn} + k_r + b_{q(r)}$

α_m = Effect of pedigree

γ_n = Effect of planting density

$\alpha\gamma_{mn}$ = Effect of pedigree and planting density interaction

k_r = Effect of Environment

$b_{q(r)}$ = Effect of experimental unit nested in environment

Data were checked for outliers using Bonferroi's corrected residuals at a p-value < 0.02, and four observations were removed from 2391 total observations. The first step in the modeling procedure was to fit all fixed effects and their interactions to each parameter of the logistic model. The next step in the modeling procedure was to fit the error structure of the model. The error structure was fit as random effects and residuals. All random effects were fitted to each parameter of the logistic model. Parameters of the logistic model were estimated using the maximum likelihood procedure. Fixed effects and their interactions for each parameter were evaluated using f-tests, and analysis of variance (ANOVA) was used to test significance for each effect. Fixed effects with a p-value greater than 0.05 were considered non-significant and dropped from the model (table 3). The fixed effects population, planting density, and their interaction were retained in the asymptote model, while population was the only fixed effect retained in the x-midpoint and scale models. In order to simplify the model, random effects with estimates close to zero were dropped from the model for each parameter. The remaining models were compared using a likelihood ratio test. After analysis, the random effects of experimental unit and environment were retained in the model for the asymptote. The effect of environment was the only random significant in the x-midpoint model, and no random effects were significant in the scale model. The variance model was written as a power variance structure, to account for the increasing variances with increased time (Pinheiro and Bates, 2000). The variance is believed to increase with some power with increasing time (Pinheiro and Bates, 2000). The model for the variance structure is as follows:

$$Var_{\,x(GDD)} = Var\,|x|^{2\gamma}$$

The maximum kernel weight was calculated from the derivative of the logistic function. Maximum growth rate was calculated by dividing the asymptote by the scale multiplied by four. A linear mixed model was fitted to maximum kernel growth rates. In this model fixed effects are represented by Greek letters, and random effects are represented by Roman letters:

Model for maximum kernel growth rate:

$y_{mnr} = \mu + \alpha_m + \gamma_n + \alpha\gamma_{mn} + k_r + \varepsilon_{mnr}$

y_{mnr} = Maximum kernel growth rate

α_m = Effect of pedigree

γ_n = Effect of planting density

$\alpha\gamma_{mn}$ = Effect of pedigree and planting density interaction

k_r = Effect of Environment

ε_{mnr} = Residual error

Fixed effects and their interactions were fitted to the model. Fixed effects were evaluated using F-Tests and the analysis of variance to test for significance. Fixed effects with p-values greater than 0.05 were considered non-significant. All random effects were fitted to the model. Random effects with estimates of zero were dropped from the model. All possible models were then compared using the AIC criterion to select the best model. Environment was the only random effect retained in the model for the maximum kernel growth rate.

Contrasts were evaluated using f-tests to compare differences in parameters derived from the logistic function. Differences between mean estimators with p-values greater than 0.05 were considered non-significant. All non-linear modeling calculations were made using R statistical software. Linear modeling was done using SAS proc mixed (SAS Institute, Cary, NC).

RESULTS AND DISCUSSION

Final kernel weight was affected by population, planting density, and their interaction (Table 1). Values and standard errors for final kernel weights are reported in Table 2. Final kernel weights were higher at low planting densities than at high planting densities for the advanced populations BSSS(R)C17 and BS13(HI)C5 (Table 3). Kernel weights remained constant over the range of planting densities used in this study for the un-advanced population BSSS (Table 3). Kernel weights of the advanced populations BSSS(R)C17 and BS13(HI)C5 populations were affected more by plant density than the un-advanced population BSSS. Grain yield decreased in the unimproved population BSSS at plant densities in excess of 5 plants m^{-2}, while grain yield of the advanced populations BSSS(R)C17 and BS13(HI)C5 increased with higher planting densities (Brekke et al, 2010). Therefore, the advanced populations BSSS(R)C17 and BS13(HI)C5 are probably better adapted to the densities used in this study that the unimproved population BSSS. Since there is a decrease in yield, but no decrease in final kernel weight over the range of planting densities used in this study, there must be a decrease in kernel number at higher plant densities. BSSS may respond to increased planting density stress by a reducing potential kernel number. BSSS(R)C17 and BS13(HI)C5 are better adapted to higher planting densities. It is possible these advanced populations maintain potential kernel number throughout the range of planting densities used in this study, and react to increases in plant density stress by decreasing kernel weight.

Final kernel weight was higher in the advanced populations BSSS(R)C17 and BS13(HI)C5 then the un-advanced population BSSS at low planting densities (Table 4). Recurrent selection for yield has increased final kernel weight at low planting densities used in this study. This may be attributed to an increased sink strength or increased assimilate supply per sink.

Final kernel weights at high planting densities were similar between the un-advanced population BSSS and the advanced population BSSS(R)C17 and BS13(HI)C5 (Table 5). In this study, kernel weights of advanced populations were more sensitive to planting density than un-advanced populations. Previous research indicates that advanced cycles BSSS(R)C17 and BS13(HI)C5 yield more at higher plant densities than un-advanced cycles (Brekke et al., 2010). Brekke et al., (2010) reports that grain yield of the unimproved population BSSS decreases while grain yield of the advanced populations BSSS(R)C17 and BS13(HI)C5 increases over the range of plant densities used in this study. Since final kernel weight of advanced populations was not higher than un-advanced populations at high planting densities, yield increases may be attributed to factors other than increased final kernel weight. These factors may include a decreased number of barren plants or an increased kernel number per unit area in advanced cycles of selection.

Kernel weights of the most advanced populations for each selection program was compared in this study. The most recent cycle of selection for the half-sib selection and reciprocal recurrent selection program are BSSS(R)C17 and BS13(HI)C5 respectively. Kernel weights were similar at both planting densities between BSSS(R)C17 and BS13(HI)C5 populations (Table 4, Table 5). Neither selection program was superior to the other for increasing final kernel weight.

The hybrids BSSS/BSSS(R)C17 and BSSS/BS13(HI)C5 both had higher final kernel weights at high and low plant densities then the average of their respective parents

(Table 6). Heterotic effects are present for final kernel weight in these populations. Therefore, that final kernel weight may be a dominantly inherited trait.

Kernel fill duration was influenced by breeding population in the Iowa Stiff Stalk Synthetic maize population (Table 1). Kernel fill duration was not influenced by planting density in the range of densities used in this study (Table 1). Values and standard errors for kernel fill duration are presented in Table 7. Kernel fill duration was longer in the advanced populations BSSS(R)C17 and BS13(HI)C5 than the un-advanced population BSSS (Table 8). Recurrent selection for yield has increased the kernel fill duration in the Iowa Stiff Stalk Synthetic maize population. This supports other studies that indicate that longer kernel fill duration may be partially responsible for increased yields in maize (Cavalieri and Smith, 1985; Gambin et al., 2007; Poneleit and Egli, 1979; Wang et. al., 1999). Longer kernel fill durations in advanced populations may be the result of lengthening the green leaf area duration or delaying the onset of senescence (Craftsbrandner and Poneleit, 1992). Increased green leaf area duration results in the leaves remaining photosynthetically active later in the growing period. This may result in increased duration of assimilate supply to the growing kernels. Increases in kernel fill duration may also be the result of increased source assimilates due to improved resource capture. Brekke et al., (2010) reported smaller tassels and more upright leaves in the advanced populations BSSS(R)C17 and BS13(HI)C5 than in the unimproved population BSSS. This may result in improved resource capture and an increased assimilate supply to the kernels.

Kernel fill duration was not increased in the F1 hybrids BSSS/BSSS(R)C17 and BSSS/BS13(HI)C5 (Table 6). Therefore, no heterotic effects were present in the

BSSS/BSSS(R)C17 and BSSS/BS13(HI)C5 crosses, indicating that kernel fill duration is an additively inherited trait.

Kernel fill rate was not influenced by population or planting density in this study. Recurrent selection for yield has not changed the rate of kernel filling or the effect of planting density on kernel fill rate in the Iowa Stiff Stalk Synthetic maize population (table not included). Our results indicate there is more variation in the duration of grain filling than in the rate of grain filling supporting previous research (Crosbie and Mock, 1981; Poneleit and Egli, 1979).

The scale parameter was influenced by population in the Iowa Stiff Stalk Synthetic maize population (Table 1). The planting density did not affect the scale parameter across the range of densities used in this study (Table 1). Scale values were higher in the advanced populations BSSS(R)C17 and BS13(HI)C5 then the un-advanced population BSSS (Table 10). The increase in scale vales may be attributed to increased kernel weights and increased duration of grain filling in advanced populations. Populations with higher kernel weights have to accumulate a greater amount dry matter to go from 50% to 75% complete compared to populations with lower kernel weights.

CONCLUSIONS

Recurrent selection for yield has resulted in changes in final kernel weights in the Iowa Stiff Stalk Synthetic maize population. Recurrent selection for yield has led to increased final kernel weights at the lower plant density used in this study. However, recurrent selection did not affect final kernel weights at the higher plant density used in this study. Other studies report that the advanced populations had a higher grain yield than BSSS at the higher plant density. Since no increases in final kernel weight were found at high plant densities, these yield increases may be attributed to other factors such as a greater kernel number in the advanced populations. This increased kernel number may be attributed to decreased barrenness or increased kernel set in advanced populations. Kernel weights of advanced populations responded more to high plant density stress than the un-advanced cycle BSSS. This may be the result of how each population reacts to high plant density stress.

Recurrent selection for yield has also increased the kernel fill duration in the Iowa Stiff Stalk Synthetic maize population. This may be attributed an increased green leaf area duration or delayed onset of senescence.

Kernel fill rate has not been changed as a result of recurrent selection for yield in the Iowa Stiff Stalk Synthetic population. Therefore, in this population there is more variation in the duration of grain filling than in the rate of grain filling. It is evident that more work is needed to determine the effect of kernel fill rate and kernel fill duration on yield.

This study also provides some evidence on the inheritability of these traits. Final kernel weight in the Iowa Stiff Stalk Synthetic maize population appears to be dominantly inherited while kernel fill duration may be additively inherited.

The results of these data support our hypothesis that recurrent selection for yield has changed grain fill characteristics in the Iowa Stiff Stalk Synthetic Maize population.

More research will be needed to determine the relationship between grain fill characteristics and yield in maize, and how planting density affects these characteristics.

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Table 1. ANOVA table for fixed effects in the statistical model containing all fixed effects. Fixed effects with p-values greater than 0.05 were dropped from the model.

Effect	Asymptote	X-Mid	Scale	Rate
Population	**	***	**	NS
Plant density	***	NS	NS	NS
Population x Plant density interaction	***	NS	NS	NS

*,**,*** Significant at the 0.05, 0.01, and 0.001 probability levels respectively.
† NS, Non-significant at p-value of < 0.05.

Table 2. Asymptotes values(grams/10 kernels) at high and low planting densities with by populations standard errors**.**

Population	7.7 Pl m^{-2}	5.3 Pl m^{-2}	Standard Error
BSSS	2.08	2.095	0.218
BSSS/BSCB1	2.029	2.26	0.216
BSSS(R)C17	2.186	2.34	0.129
BSSS(R)C17/BSCB1	2.075	2.213	0.207
BSSS/BS13(HI)C5	2.262	2.368	0.16
BSSS/BSSS(R)C17	2.25	2.35	0.127
BS13(HI)C5	2.179	2.358	2.358
BS13(HI)C5/BSCB1	2.06	2.252	0.215

Table 3. P-values for contrasts comparing asymptote values at high and low density for each population.

Population	p-values
BSSS	NS
BSSS/BSCB1	**
BSSS(R)C17	***
BSSS(R)C17/BSCB1	NS
BSSS/BS13(HI)C5	NS
BSSS/BSSS(R)C17	*
BS13(HI)C5	**
BS13(HI)C5/BSCB1	*

*,**,*** Significant at the 0.05, 0.01, and 0.001 probability levels respectively.
† NS, Non-significant at p-value of < 0.05.

Table 4. P-values comparing asymptote values at low planting densities of different populations.

Population 1	Population 2	P-value
BSSS/BSCB1	BSSS	*
BSSS(R)C17/BSCB1	BSSS	NS
BS13(HI)C5/BSCB1	BSSS	*
BSSS(R)C17	BSSS	***
BSSS/BS13(HI)C5	BSSS	***
BSSS/BSSS(R)C17	BSSS	***
BS13(HI)C5	BSSS	***
BS13(HI)C5	BSSS(R)C17	NS
BSSS/BS13(HI)C5	BS13(HI)C5	NS
BSSS/BSSS(R)C17	BSSS(R)C17	NS

*,**,*** Significant at the 0.05, 0.01, and 0.001 probability levels respectively.
† NS, Non-significant at p-value of < 0.05.

Table 5. P-values for contrasts comparing p-values at high planting densities of different populations.

Population 1	Population 2	P-value
BSSS	BSSS/BSCB1	NS
BSSS(R)C17/BSCB1	BSSS	NS
BSSS	BS13(HI)C5/BSCB1	NS
BSSS(R)C17	BSSS	NS
BSSS/BS13(HI)C5	BSSS	**
BSSS/BSSS(R)C17	BSSS	**
BS13(HI)C5	BSSS	NS
BS13(HI)C5	BSSS(R)C17	NS
BSSS/BS13(HI)C5	BS13(HI)C5	NS
BSSS/BSSS(R)C17	BSSS(R)C17	NS

*,**,*** Significant at the 0.05, 0.01, and 0.001 probability levels respectively.
† NS, Non-significant at p-value of < 0.05.

Table 6. Tests for heterosis.

Populations	Parameter	F-Value	P-Value
BSSS/BSSS(R)C17	Asymptote (5.3 Pl m^{-2})	23.57	***
	Asymptote (7.7 Pl m^{-2})	8.412	***
	X-Mid	0.81	NS
	Scale	1.41	NS
BSSS/BS13(HI)C5	Asymptote(5.3 Pl m^{-2})	6.26	*
	Asymptote(7.7 Pl m^{-2})	5.105	*
	X-Mid	0.211	NS
	Scale	0.03	NS

*,**,*** Significant at the 0.05, 0.01, and 0.001 probability levels respectively.
† NS, Non-significant at p-value of < 0.05.

Table 7. Values for x-midpoints with standard errors.

Population	X-Mid(GDD)	Standard Error
BSSS	574.97	6.42
BSSS/BSCB1	560.42	8.87
BSSS(R)C17	617.16	5.54
BSSS(R)C17/BSCB1	558.32	8.37
BSSS/BS13(HI)C5	590.37	6.79
BSSS/BSSS(R)C17	602.46	5.96
BS13(HI)C5	598.05	7.58
BS13(HI)C5/BSCB1	562.78	9.07

Table 8. P-values of contrasts comparing x-midpoints of different populations.

Population 1	Population 2	P-value
BSSS	BSSS/BSCB1	NS
BSSS	BSSS(R)C17/BSCB1	NS
BSSS	BS13(HI)C5/BSCB1	NS
BSSS(R)C17	BSSS	***
BSSS/BS13(HI)C5	BSSS	NS
BSSS/BSSS(R)C17	BSSS	**
BS13(HI)C5	BSSS	*
BSSS(R)C17	BS13(HI)C5	*
BSSS(R)C17	BSSS/BSSS(R)C17	NS
BSSS/BS13(HI)C5	BS13(HI)C5	NS

*,**,*** Significant at the 0.05, 0.01, and 0.001 probability levels respectively.
† NS, Non-significant at p-value of < 0.05.

Table 9. Values for scale parameter with standard errors.

Population	Value(GDD)	Standard Error
BSSS	112.1	3.34
BSSS/BSCB1	112.54	4.14
BSSS(R)C17	123.88	2.66
BSSS(R)C17/BSCB1	110.73	3.61
BSSS/BS13(HI)C5	118.57	3.33
BSSS/BSSS(R)C17	122.2	2.78
BS13(HI)C5	126.52	3.8
BS13(HI)C5/BSCB1	115.38	4.06

Table 10. P-values of contrasts comparing scale values for two separate populations.

Population 1	Population 2	P-value
BSSS	BSSS/BSCB1	NS
BSSS	BSSS(R)C17/BSCB1	NS
BS13(HI)C5/BSCB1	BSSS	NS
BSSS(R)C17	BSSS	**
BSSS/BS13(HI)C5	BSSS	NS
BSSS/BSSS(R)C17	BSSS	*
BS13(HI)C5	BSSS	**
BSSS(R)C17	BSSS(R)C17/BSSS	NS
BSSS(R)C17	BS13(HI)C5	NS
BSSS/BS13(HI)C5	BS13(HI)C5	NS

*,**,*** Significant at the 0.05, 0.01, and 0.001 probability levels respectively.
† NS, Non-significant at p-value of < 0.05.

CHAPTER 5 GENERAL CONCLUSIONS

The main conclusion of this study is the confirmation of our hypothesis that recurrent selection has changed grain fill characteristics and their response to planting density.

The Iowa Stiff Stalk Synthetic maize population program used yield as the criterion for recurrent selection. While selecting for increased maize grain yield, grain fill characteristics were indirectly altered in this population. Recurrent selection for yield in the Iowa Stiff Stalk Synthetic maize population has resulted in the increased kernel dry weight at low planting densities and increased kernel fill duration. There was no difference between populations in kernel dry weight at high planting densities which indicates increased yields have come from factors other than increased kernel dry weight. These other factors may include decreased barrenness or increased kernels per ear in advanced cycles compared to un-advanced cycles. Kernel fill duration has also been increased with recurrent selection for yield in the Iowa Stiff Stalk Synthetic maize population.